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XV.—*On the Mechanism of Aquatic Respiration, and on the Structure of the Organs of Breathing in Invertebrated Animals.* By Thomas Williams, M.D., F.L.S., Physician to the Swansea Infirmary.

[Concluded from vol. xvii. p. 258.]

[With a Plate.]

*Cephalopoda**.

The Cephalopod Mollusks stand at the head of the Invertebrated series, not only in virtue of a superiority of bodily form, but also of the higher type of structure which pervades their entire organization. They depart from the Gasteropods in the position and shape of their principal prehensile and locomotive organs, and in the significant fact that in them the 'general cavity' of the body is almost obliterated. They approach the Vertebrated animal in the following respects:—They possess a rudimentary endoskeleton, greatly developed cephalic ganglions, large and active organs of sense, a vigorous and well-formed muscular system, a blood-vascular apparatus more perfect than that of any other class of Invertebrata, a nutritive fluid thickly fibrinized and of high specific gravity, and blood-corpuscles which in figure and structure more nearly resemble those of the Mammal than do those of any other Invertebrated animal. The circulatory apparatus of the Cephalopods does not, however, constitute a perfectly closed system. This point was established by the early classic researches of Professor Owen. The cephalic venous sinus, and

* The author regrets that, in consequence of various engagements, he has been obliged to postpone so long the publication of this last paper, which completes the series published in the 'Annals' under the above title from time to time during the years 1854–1856.

its continuation, the great anterior vena cava, appear to form closed-off portions merely of the peritoneal cavity. The vena cava in *Nautilus* is a flattened spacious channel, the parietes of which are perforated by numerous orifices which communicate directly with the peritoneal cavity. This remarkable peculiarity is thus described by Professor Owen: "There are several small intervals left between the muscular fibres and the corresponding round apertures in the membrane of the vein (vena cava) and contiguous peritoneum, by which the latter membrane becomes continuous with the lining membrane of the vein; from this structure it would seem that the *blood might flow into the peritoneal cavity*, or the fluid contents of that cavity be absorbed into the vein*."

Though, from the small size of the specimens upon which the author's observations have been conducted, he has not been successful in his attempts to verify the statements of Prof. Owen, he thinks it very probable, on the ground of analogy, that they are true. In the Echinoderms and Annelids the vascular system undoubtedly communicates with the peritoneal cavity. Of the Gasteropod Mollusks Milne-Edwards observes, "L'artère aorte, parvenue au point où le canal digestif se recourbe pour descendre de la face supérieure du bulbe pharyngien dans la cavité abdominale, *débouche directement dans une vaste lacune*, dont les parois sont formées en partie par les téguments communs de la tête et en partie par les muscles et les tuniques du pharynx jointes à les lames de tissu connectif étendues transversalement au devant de la cavité abdominale†." The cephalic sinus in the Gasteropods forms a part of the arterial system; in the Cephalopods it is a segment of the venous system. That portion of the circulatory system of the Cephalopod which is intermediate, *in the solids of the body*, between the arteries and veins, partakes much more strikingly of the capillary character, or less of the lacunose, than it does in any other Mollusk. It seems, from the researches of Prof. Owen, that in *Nautilus* and *Octopus*, and other genera, the pericardium (or that membrane which embraces the large central vessels) opens immediately into the branchial chamber. Dr. Lacaze Duthiers‡ has lately shown that the pericardial chamber in the Lamellibranchiata also opens externally. From these analogies the writer of this paper believes that the lung-sac of the pulmonary Gasteropods should be looked upon as the pericardial bag slightly diverted from the character which is normal to it in other Mollusks.

Considered from this homological point of view, the lung of

* Cyclop. Anat. and Phys., Art. Cephalopoda.

† Ann. d. Sc. Nat. 3 sér. 1847.

‡ Ann. d. Sc. Nat. No. 5, 1855.

the Pulmonata should be described as the pericardium, receiving air instead of water into its interior. The vascular system of Insects is filled with air, that of the Annelids with fluid. Insects differ from the Annelids, therefore, precisely in the same manner as the Pulmonata differ from other Mollusks. But, notwithstanding the express provisions which are thus made to introduce the external element into the recesses of the body of Cephalopods, these Mollusks are furnished with branchial organs more beautifully and elaborately constructed than those of any other Invertebrated animal.

The general anatomy of this class is well known. The author therefore will at once proceed to state the results of his special researches on the minute structure of the respiratory organs.

Mechanism of the Branchial Chambers.

The branchial chamber of the Cephalopod is a perfect hydraulic mechanism. It is placed in advance of the viscera. It is enclosed laterally by the mantle, the muscles of which have received an express disposition with reference to the rhythmic respiratory movements which it is designed to perform. Anteriorly the chamber is provided with two valvular openings, the valves being so arranged as to afford a ready entrance to the inspiratory water-current, and to prevent its reflux. The water thus drawn or sucked into the breathing-chamber is drawn or sucked also into the hollow axes of the gills (especially in *Octopus*) by a diastolic movement of these organs which seems to be synchronous with that of the mantle. Having freely permeated the branchiæ, the water is expelled through the funnel by an expiratory act in which the gills and the mantle contract simultaneously. The rectum and the ducts of the generative system terminate in this chamber at the base of the funnel. The expiratory current thus conveys externally the excreta. In this character, as is well known, the Cephalopods coincide with the Gasteropods.

The *precise mode* in which the water, during the respiratory movements, traverses the branchiæ, has only recently become known to the author*. It does not enter, as he formerly supposed,

* In a former paper (see Annals, ser. 2. vol. xvi. pl. 9) I introduced a figure (fig. 7) illustrative of the manner in which I then believed the water to pass through the branchiæ in the act of respiration. Although it was intended only to convey a *general* idea of the mechanism of the chamber and its currents, yet as that figure stands, it may lead to error. The hollow axes of the gills are not *open*, as there represented, at their posterior or attached extremity, but *conically closed*, as they are at the anterior extremity. It will be evident, in the text, that the water cannot therefore enter the interior of the organ in *one* large stream, as there shown.

as *one* current at the posterior extremity, but from above downwards, from the dorsal to the ventral side, in as many streams as there are spaces (Pl. XV. fig. 1 *e*) between the secondary lobuli of the organs. By this arrangement the inspiratory pure current is first and at once brought into contact with that half of the gill on which the vascular laminæ are suspended. It effects its escape, during the systole of the organ, at the ventral side, through the fissures between the *non*-vascular supports of the lobuli (*d, d*). Although in the genus *Loligo* the gill (fig. 3, 3^2) does not fold so much upon itself as to enclose a cylindrical axis, as in *Octopus* (fig. 1), the water-currents observe precisely the same direction in both. The admission of the aërating element apparently into the interior of the gill in the Cephalopods may be said, on the one hand, to be parallel to what occurs in the Lamellibranchiata, or, on the other, may be likened to the entrance of the air, in the Mammal, into the lungs. As a respiratory mechanism, it resembles the latter more than the former. The lungs possess the property of dilating and contracting, in order to inhale and exhale the gases concerned in respiration. The branchiæ of the Cephalopod are endowed with the same property. They bear a nearer similarity to the gills of the Pectinibranchiata than to those of any other Mollusks. They are highly muscular and irritable : the disposition of the muscles will be afterwards described. On the floor of the branchial chamber, situated immediately underneath each gill, and running parallel with these organs, may be observed a dense prominent *ridge* (Pl. XV. fig. 1 *h, h*), to which the branchiæ are attached, and upon which they rest. This ridge consists of a dense bundle of muscles, which during contraction are capable of approximating closely together the two extremities of the branchiæ—in other words, of shortening these organs in length. These muscles are richly supplied with nerves from the neighbouring pallial ganglion. They aid in a very material manner the branchial movements of dilatation and contraction. They not only afford a fixed point of attachment to the gills, but they are accessory to the mantle in the respiratory movements.

Structure of the Branchiæ.

The Tetrabranchiate and Dibranchiate orders are founded simply upon the number of the gills*. No classification has been attempted on the basis of the remarkable varieties which occur in the anatomical structure of the gills. As far as the

* The second pair of branchiæ in the Tetrabranchiate Cephalopods are most probably parallel to, and representative of, the *supplementary gills* of the Lamellibranchiata described in a former paper.

author's examinations have extended, he has succeeded in establishing only two main varieties,—that of *Octopus* and *Sepia* (Pl. XV. fig. 1), in which the secondary lobuli circumscribe a hollow axis, by curving from the dorsal to the ventral aspect; and that, 2ndly, of *Loligo* and *Loligopsis* (Pl. XV. fig. 3, 3^2), in which the secondary parts of the organ pass only half-way round, and float freely in the branchial chamber, instead of being, as in *Octopus*, tied down to the longitudinal pallial muscle upon which the gills rest. He has no doubt, however, that other modifications of structure in the branchial organs of this class exist; but, in consequence of the want of specimens, he is not at present in a position to speak of them. The Dibranchiate order is thus obviously resolvable into two well-marked suborders,—the one in which the gill forms a *cylinder*; the second, in which it forms a *hemicylinder*. This distinction has never before been noticed.

No example of the Tetrabranchiata has ever fallen under my notice. Prof. Owen states that they stand in closer connexion with the Gasteropod Mollusks than the Dibranchiata. In *Nautilus Pompilius* this distinguished observer figures the branchiæ as having a completely formed cylindrical arrangement.

It must therefore be concluded that the Tetrabranchiata are lower than the Dibranchiata in the Molluscan scale, and that *Octopus* should stand beneath the *Calamary* in zoological rank. This interesting fact, as the ground of classification, is commended to the attention of those who may enjoy opportunities of studying the organization of this most interesting class of animals. In accordance with this view, which regards the gill of *Octopus* as ranking below that of *Loligo*, let us proceed first to the detailed description of the lower variety.

The gills in the genus *Octopus* are strikingly distinguished in apparent structure from those of the other families of the Dibranchiate tribe. Although only two in number, in all the species of this order they exhibit, as stated before, very extraordinary diversities of shape. In the size and disposition of the branchial chamber there is no corresponding variation: it is nearly the same in all species. In *Octopus* the branchia on either side is attached in a peculiar manner to the ventral wall of the breathing-chamber. The dorsal surface is free and unattached: it is so situated as to float on a thin supporting ridge. The water thus rushes into and out of its interior with equal facility. The branchial artery, or afferent venous trunk (fig. 1 *b*), lies on and courses up along the ventral side of the organ: it emanates from the branchial hearts*. The branchial

* It will afterwards be shown that these cordiform dilatations of the blood-channels in the vicinity of the branchiæ may be viewed as mere safety

vein or efferent trunk (fig. 1 *a*) runs along the dorsal border of the gill, and terminates in the aorta (these two trunks are seen in section, fig. 2 *a, b*). These two longitudinal trunks constitute the framework by which the entire apparatus of the gill is supported. To them are attached respectively the two ends of the secondary lobuli in *Octopus*: in *Loligo*, as will be again explained, a slight variation from this type occurs. The *plan* of this structure is readily understood on a transverse section of the gill (fig. 2). In the gill of *Octopus vulgaris* there are twelve pinnæ or secondary lobuli on either side (fig. 1 *d, d*). Along the external and internal margins respectively (fig. 2 *i, i,* & *e, e*), efferent and afferent vessels are observed to travel. These secondary branches, like the primary trunks from which they proceed, serve to support, in their turn, the tripinnæ (*g*), or the ultimate leaflets in which are distributed the final capillaries of the branchiæ. As observed by Professor Owen, the gills of this Cephalopod are tripinnate. This general term, however, serves but very rudely to express the extreme refinement of structure and arrangement which these organs exhibit. The secondary and tertiary divisions are so much longer than the straight space between the points to which they are fixed, that in the ordinary state of the animal, after death, they present remarkably complex foldings and convolutions; but when the organ is in the condition of full and complete distension (with blood in the vessels and water in the hollow axis), the secondary lobuli and their appended system of leaflets are straight or smooth laminæ of exquisite slenderness, delicacy, and translucency. Although the secondary divisions (fig. 1 *d, d*) amount to no more than twelve in number on either side, the tertiary laminæ (*c, c*) which each of them supports are as many as from twenty-five to thirty on either side. The multiplication thus insured is extraordinary. The secondary lobuli are separated from each other by free, open water-passages (fig. 2 *h*). It is through these spaces that the fresh inspiratory streams enter the axial interior of the gill (fig. 2). No exact parallel to these spaces is found in any other Mollusk. The water, indeed, rushes between the secondary divisions of the gills in all the Pectinibranchiata. In these latter, however, the organ does not circumscribe a hollow interior. The tertiary branchial foliage is disposed at right angles on the secondary, just as the latter rest at right angles on the main primary trunks. According to this arrangement, no obstacle is offered to the rapid and free passage

receptacles for the retrogressing column of blood (which is either stopped or thrown back in its course during the *extreme* changes of size which the gills are constantly undergoing), with quite as much propriety as they are now considered to be propulsive hearts.

of the water-current through the gill, above from the outside to the inside, below from the inside to the outside. In a mechanical point of view, there is much to admire in this contrivance. The more forcibly the water is caused to pass through the branchia, the more completely its delicate leaflets are straightened and rendered smooth. All danger from mechanical injury is thus obviated.

The water is drawn into the hollow interior of the gill much more slowly than it is driven out. No violence to the slender structures of the organ can accrue from its forcible ejection, since the spaces through which the water effects its exit are bounded only by tendon and fibrous tissue. Now, it may be asked with great reason, how is it that during the expiratory shortening of the gill, the water does not again escape through the passages by which it entered? It is not difficult to answer this question. When the large longitudinal muscle (fig. 1 *h, h*; fig. 2 *c*) which is situated underneath the gill contracts, and thus approximates the two ends of the gill, it brings the dorsal half of the organ closer together, forming the concavity of a curve, while it separates the ventral half, which for the instant forms the convexity of the curve. At this instant the expiratory current escapes. Reversing this movement, it is not difficult to perceive how the act of inspiration occurs.

The gills of all Cephalopods are remarkably elastic; at one moment exhibiting an extraordinary capability of dilatation, at another of extreme contraction. This property is due to the presence of muscular fibres. They are distributed throughout the entire structure of the gill; they embrace the vessels; they course along the edges of the laminæ; they are internally intermingled with elastic tissue, whose normal mode of action is rhythmic; they contribute in a most important manner to the mechanism of breathing.

The branchial system of the Cephalopods is distinguished by one further peculiarity:—in no instance yet examined has the presence of vibratile cilia been proved. In this particular they are allied to the gills of the Crustacea and the Fish*. In the Cephalopod, no part whatever of the gill is furnished with cilia. At first it might be thought that its extreme flexibility superseded the necessity for such organules. The instance of the Crustacean gill, however, which is perfectly passive, disproves this imagination. *Why* cilia are denied to the branchiæ of the Cephalopod, cannot at present be explained. The fact is attested by all observers.

* I am sorry that, in consequence of the want of specimens, I cannot, from personal knowledge, state at this moment whether the gills of the Pectinibranchiata are ciliated or not.

The *ultimate laminæ* (fig. 4 *g, g*) are arranged in a dense parallel series on either side of the secondary processes. They present the same disposition as those of the gill of the Crab. Those of the latter, however, are comparatively stiff leaves; those of the former are contractile and flexible in the highest degree. The tissue of the Cephalopod gill is extremely extensile, that of the Crab is fixed and passive.

It is very difficult to obtain a satisfactory view of the fully-unfolded flat surface of one of these ultimate laminæ; but with care, it may be obtained. Each lamina is constructed very much on the plan of that of a Pectinibranchiate gill. It is a leaflike structure, bearing two strata of vessels (fig. 6 *a, b*), an afferent and an efferent, which double the one into the other at the free margin (*c, c*). The aërating current laves thus the advancing and the returning capillary streams of blood. The ultimate blood-channels (figs. 5, 6) bear an exact resemblance to those already described in the gills of the Pectinibranchiata. They are parallel, non-dividing channels, of *unvarying diameter*. At the point of curving (*c, c*), or the free margin, they do not dilate, as in the case of the Lamellibranchiata. From all others they are distinguished by the circumstance of their extreme distensile and contractile capabilities. If these ultimate vessels united and divided in a retiform manner, they would approach to the plan observed in the branchiæ of the Fish. They form, however, a straight parallel series, laminarly blended together by delicate cellular tissue (fig. 6). In this character they conform to the Molluscan distinctive type of structure. No instance of departure from this type is known, from the Tunicate to the Cephalopod. From the Pectinibranchiate standard they differ in the absence of cilia. The absence of cilia is compensated in the Cephalopod by the extreme muscularity of the organ.

It is *scarcely possible* in the branchial organs of this class to arrive at a certain knowledge as to the point whether the ultimate laminæ are covered or not by an epithelium. The parts are so irritable and transparent, that the question cannot with confidence be determined. That they are not lined by a *ciliated* epithelium is quite certain; that they are not invested by any epithelium at all, is improbable; but the existence of this covering cannot be demonstrated convincingly. The conclusion must therefore rest on general analogy: all analogy is unquestionably in favour of its presence.

The branchiæ of *Loligo* (fig. 3, 3^2) differ from those of *Octopus* (fig. 1) in a remarkable manner. In the latter genus the secondary divisions (*c, c*) are attached to the ventral aspect of the organ (fig. 2 *i, i*). In the former they are loose, and float freely in the branchial cavity (fig. 3 *b, b*, & 3^2 *c, c*). They thus form